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A REVIEW OF THE LITERATURE ON THE MOUNTAIN BEAVER

UNITED STATES DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE
BUREAU OF SPORT FISHERIES AND WILDLIFE
Special Scientific Report--Wildlife No. 78

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A REVIEW OF THE LITERATURE ON THE MOUNTAIN BEAVER

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Branch of Wildlife Research
Bureau of Sport Fisheries and Wildlife
Fish and Wildlife Service
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UNITED STATES DEPARTMENT OF THE INTERIOR

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ABSTRACT

This report summarizes the available knowledge about the mountain beaver, Aplodontia rufa, and lists some 260 literature references. Since the first account in 1805, from the Lewis and Clark expedition, a considerable literature has accumulated, much of which is no longer generally available. The mountain beaver, considered the most primitive of living rodents, is found only on the Pacific coast of North America. Type localities and ranges of the seven races are listed.

Frontispiece. The mountain beaver (Aplodontia rufa)
(Photo by Weyerhaeuser Co.)

A REVIEW OF THE LITERATURE ON THE MOUNTAIN BEAVER

The mountain beaver, Aplodontia rufa (Rafinesque), has attracted interest among taxonomists and naturalists since it first appeared in the accounts of Lewis and Clark in 1805. The only representative of the monotypic family Aplodontidae, it is considered to be the most primitive of living rodents. It is found only on the Pacific Coast of North America, from British Columbia to Central California.

Much has been written on the mountain beaver's taxonomy and natural history, but these writings are scattered throughout the literature and include rare manuscripts that are not generally available. No major treatise has been written on this interesting and peculiar rodent.

The purpose of this review is to summarize available knowledge for reference use in study and research and to consolidate the many brief and scattered references.

The study was based mainly on an extensive search of the literature. It entailed the review and analysis of some 260 collected and collated references. References were examined at the following libraries: (1) In Washington, D. C. -- the Library of Congress, Department of Agriculture, Department of the Interior, Smithsonian Institution, and the U. S. National Museum; (2) in Maryland -- the Patuxent Wildlife Research Center at Laurel and the Agricultural Research Center in Beltsville; (3) in Colorado -- the Denver Wildlife Research Center and the U. S. Geological Survey Library at the Denver Federal Center; and (4) in Washington State -- the Forest Research Center in Olympia. Where references were not available for examination, they were cited from authoritative sources.

The following biologists contributed valuable advice on preparation and review of the study: Dan L. Campbell, Wendell E. Dodge, and Harry D. Hartwell at the Olympia Forest Research Station, Olympia, Washington; Victor B. Scheffer at the Mammal Biological Laboratory, Bureau of Commercial Fisheries in Seattle; Nelson B. Kverno, and Cecil S. Williams at the Denver Wildlife Research Center; Kenneth J. Chiavetta, Charles F. Kaczynski, Louis N. Locke, and Lucille F. Stickel at the Patuxent Wildlife Research Center; Richard H. Manville at the National Museum; and C. Edward Carlson, Eugene H. Dustman, Walter W. Dykstra, and Lee E. Yeager in the Office of the Branch of Wildlife Research.

Dr. William H. Lawrence, Biologist of the Weyerhaeuser Company, Centralia, Washington, and Wendell E. Dodge kindly supplied photographs.

HISTORICAL NOTES

First mention of the mountain beaver was in the journal of Captain William Clark, written during the famous transcontinental expedition of 1805. The following entry appears in Clark's notes dated Friday, December 13, 1805, in winter quarters at Fort Clatsop (now Astoria, Oreg.):

> "The Clatsops leave us today after a brackfast of Elk, which they appeared to be very fond of before they left us they Sold me two robes of the skins of a Small animal about the size of a cat, and to Captain Lewis 2 Cat or Loucirva Skins for the purpose of makeing a Coat."

When the explorers questioned the Chinook Indians about the "2 Cat or Loucirva Skins" they were informed that the "Skins" were "she-wal-lal." Because of imperfect language communications, Clark wrote sewellel as the Chinook name of the "Skin." However, the Chinook name "she-wal-lal" did not apply to the animal itself, but to the blanket or robe made from its skin. The faulty name sewellel recorded by Clark first appeared in the Biddle-Allen narration of the Lewis and Clark's expedition in two volumes (1814). The following notice is found in the Allen edition:

> "Sewellel is a small animal found in the timbered country of this coast. It is more abundant in the neighborhood of the great falls and rapids of the Columbia, than on the coast which we inhabit (mouth of the Columbia). The natives make great use of the skins of this animal in forming their robes, which they dress with the fur on, and attach them together with sinews of the elk or deer; the skin, when dressed, is from fourteen to eighteen inches long, and from seven to nine in width; the tail is always separated from the skin by the natives in making their robes. This animal mounts a tree [Audubon and Bachman (1854), and Suckley and Gibbs (1860), regard this statement "mounts a tree" as erroneous] and burrows in the ground precisely like a squirrel; the ears are short, thin and pointed, and covered with a fine short hair, of a uniform reddish brown: the bottom or base of the long hairs, which exceed the fur but little in length, as well as the fur itself, are of a dark colour next to the skin for two thirds of the length of this animal: the fur and hair are very fine, short, thickly set, and silky; the ends of the fur and tips of the hair, are of a reddish brown, and the colour predominates in the usual appearance of the animal."

The following quotation is from Rees of London (1814):

> "Captain Lewis offered considerable rewards to the Indians, but was never able to procure one of these animals alive."

From Lewis and Clark's account of the sewellel, Rafinesque (1817), named the animal Anisonyx (?) rufa. His account reads:

> "Anisonyx ? rufa Raf. Fur long, silky, entirely reddish brown, ears short, pointed with short hair - Obs. This animal called Sewellel by Capts. Lewis and Clark, is of a doubtful genus, since they only saw the fur of it; it burrows and runs on trees like the ground-squirrels; length eighteen inches, found in the neighborhood of the Columbia River."

Rafinesque's Anisonyx brachiura was based upon Lewis and Clark's burrowing squirrel and Anisonyx rufa upon their sewellel. Also, on the same page, Rafinesque names Lewis and Clark's "barking squirrel," Cynomys ludovicianus, now known as the prairie dog. The genus Anisonyx referred to Lewis and Clark's "burrowing squirrel," since ascertained by taxonomists to be another species of prairie dog (Cynomys columbianus); hence a synonym for Anisonyx brachiura.

Due to the misunderstanding by Rafinesque of Lewis and Clark's meaning of these two mammals, Harlan (1825) transferred the name sewellel (Anisonyx rufa) to the genus Arctomys, but retained the specific name rufa because it applied to the sewellel's external description. However, Coues (1876) pointed out that naturalists constantly adopted and retained scientific names given upon a known basis, even when such names were unqualified by diagnosis. Therefore, he reasoned it invalid for Harlan to change the generic designation of sewellel and continued to use sewellel for the mountain beaver.

In 1829, Sir John Richardson became the first naturalist to study a mountain beaver skin. His description was based on specimens collected by David Douglas, from which he characterized Aplodontia leporina.

> "M. Rafinesque has given few details on the genus Anisonyx, and says of the teeth, merely, that they resemble those of the squirrels. This character does not apply at all to the Sewellel, which was known to Rafinesque only from Lewis and Clark's description. I have, therefore, been induced to constitute a new genus for the reception of this animal, and as the specific name of rufa is quite inapplicable, I have given it one derived from the general resemblance it bears to animals of the hare kind."

From dentition, examination of the mandible, cranial measurement differences, and white interspersed hairs in another specimen, Richardson alluded to the possible existence of a second species. He wrote the following account:

> "The specimen is not sufficiently perfect to enable me to give it characters as a distinct species, but I have little doubt of its being so."

The existence of Richardson's second species has never been verified or disproved.

From the time of Richardson's account, it was not until 1848 that specimens were reported again. The naturalist T. R. Peale of the Wilkes Exploring Expedition collected two mountain beaver specimens in the neighborhood of Puget Sound, which he described. He also discussed their habits and abundance in that area.

Soon after, in 1854, Audubon and Bachman quoted Lewis and Clark's account as first published. They also summarized Richardson's work, made inferences drawn from the anatomy as to the animal's habits, and added some statements concerning its distribution.

Under the supervision of Spencer F. Baird (1857), the naturalists J. S. Newberry, J. E. Cooper, G. Suckley, and G. Gibbs of the Pacific Railroad Explorations gathered material and made valuable observations on the distribution and habits of the mountain beaver. Baird suggested that Rafinesque's specific name rufa be accepted as the proper specific name of the species, and Coues (1877) adopted it as such.

From salient internal characters similar to those of the beaver (Castor canadensis), Baird (1858) placed the animal in the subfamily Castorinae of Sciuridae.

In 1864, Peters of the Berlin Museum described a California mountain beaver as a new race, to which he applied the name Haplodon leporinus var. californicus, said to have come "aus den Gebirgen Californiens."

On the basis of original anatomical studies and a review of the literature, Coues (1877), in his comprehensive monograph, adopted the genus Haplodon for the mountain beaver.

In 1886, Merriam described a species of mountain beaver (Aplodontia major), from California and in 1899 described four more races: A. pacifica, A. phaea, A. olympica, and A. major rainieri.

In 1914, Kellogg and Taylor described two additional mountain beavers from California: A. chryseola Kellogg, and A. nigra Taylor. Two years later, Taylor described three more races: A. californica columbia, A. rufa grisea, and A. humboldtiana.

Monographic studies of the life history of the mountain beaver include those of H. E. Anthony (1916), Charles L. Camp (1918), Theo. H. Scheffer (1929), and Walter P. Taylor (1918). Taylor summarized the full taxonomic history of the genus.

EVOLUTION

Little is known of the affinities of the superfamily Aplodontoidea and its monotypic representative, Aplodontia rufa, among the Rodentia. Taylor (1918) wrote that the family Aplodontidae is exclusively North American in origin, development and present distribution. The mountain beaver is the only living member of the family and is generally considered to be the most primitive of living rodents.

Wilson (1949) pointed out that the known geologic history of the Aplodontidae is from the Upper Eocene to Recent. Taylor (1918) remarked that the former range of the Aplodontidae was greater than that at present, but conceded that little is known of the relationships of the early aplodontiids to the present species. He stated that its ancestry dates to the earliest aplodontiid genus Allomys which was discovered in the Oligocene deposits of the Middle John Day Region in Oregon. Matthew (1904) recovered an undetermined species of Allomys from the Lower Miocene of South Dakota.

From mandibular and dental characters, Schlosser (1924) described Aplodontia asiatica which he believed to be an authentic record of a Tertiary aplodontiid from Mongolia. However, Miller (1927) doubted the affinity of Schlosser's Mongolian species to the aplodontiid stock. He compared characters of the ramus in Liodontia and Aplodontia, and found that the animal represented a member of the dipodine group. Miller ascribed Schlosser's animal to the genus Pseudoplodon. Gazin (1932) compared specimens of Liodontia with Schlosser's species and suggested that the latter had separated from the aplodontiid stock at a time when development had reached a stage between Meniscomys and Liodontia (fig.1).

McGrew (1941) pointed out that there were no characters separating Aplodontidae from Ischyromyoidae. He recognized two phylogenetic lines from Eohaplomys to Aplodontia and Mylagaulus. McGrew stated that the direct line from Eohaplomys to Aplodontia represented the basic stock and was of family rank, whereas the offshoot from Promylagaulus to Mylagaulus represented extreme divergence and adaptive specialization and should be ranked in the family Mylagaulidae.

Figure 1 illustrates McGrew's systematic arrangement of the primitive aplodontiid stock.

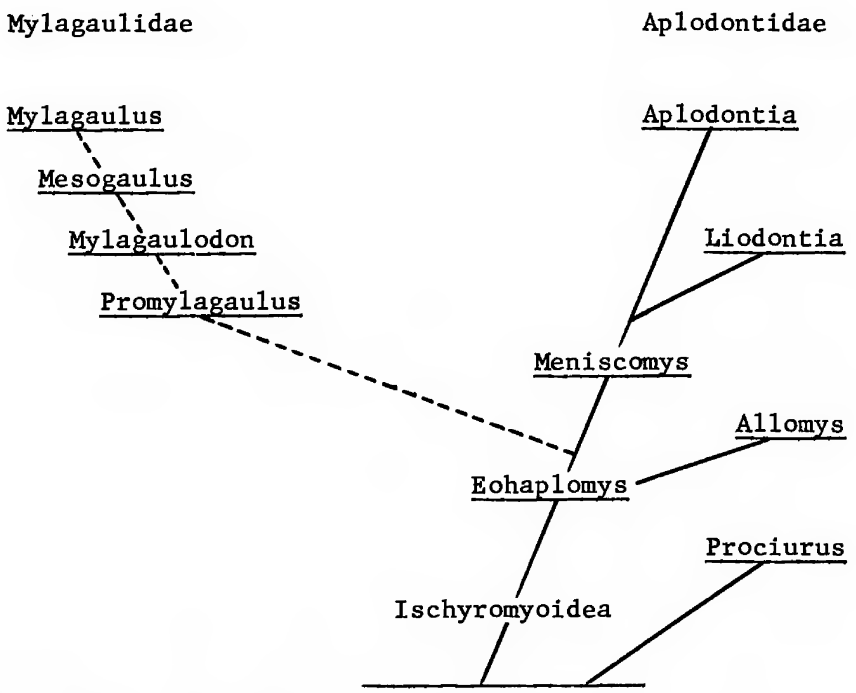

Figure 1. Relationships of the primitive aplodontiids (after McGrew)

DISTRIBUTION

The known past and present distribution of the mountain beaver is unique in that its range is limited to a small strip of heavy rainfall along the Pacific Coast from British Columbia to central California (fig. 2). Not only is its range limited but so far as is known, every fossil form which might be ancestral to it also came from the same general area.

Matthew (1915) stated that such distribution cannot be explained by the principles of mammalian dispersal, where mammalian evolution and migration are stimulated primarily by climatic and environmental changes. He wrote:

> "A species should be at first most progressive at its point of original dispersal, and continue this progress at that point in response to whatever stimulus originally caused it and spread out in successive waves of migration, each wave a stage higher than the previous one at any one time, therefore, the most advanced stages should be nearest the center of dispersal, the most conservative stage farthest from it."

McGrew (1941) said that the mountain beaver presents a picture exactly the opposite of that required by the Matthewsian hypothesis. He also said that the present range of the mountain beaver is apparently near the center of origin and distribution of the family Aplodontidae. Furthermore, he suggested that the distribution of the mountain beaver cannot be accounted for by climatic or environmental change at the center of dispersal because environmental conditions along the Pacific Coast might have been quite stable during Tertiary time, or at least stable enough to allow the mountain beaver to maintain its range with relatively little structural modification. McGrew said that those that migrated did so either because of population pressure or the inherent tendency of all animal life to expand. Those that were not successful in adapting to new environment became extinct, or their range became restricted.

RACES AND RANGE

Figure 2 illustrates the present distribution of the mountain beaver. Taylor (1918) recognized wide individual variation, as well as considerable geographical variation. Thus, mountain forms are generally larger than nearby lowland or coastal forms. The most strikingly colored form is the geographically isolated Aplodontia rufa nigra of Point Arena, California.

Taylor (1918) revised the 13 races of the mountain beaver and listed nine, four of which occurred in the State of Washington. Finley (1941) also recognized four races in Washington. Dalquest and Scheffer (1945) concluded as a result of their investigation on specimens from the Biological Survey Collection, Washington, D.C., and on specimens in the Museum of Vertebrate Zoology, that there were only two recognizable races in Washington: rufa in western Washington and rainieri in the Cascades. Miller and Kellogg (1955) and Hall and Kelson (1959) also recognized these two races in Washington. The type locality and distribution of the seven races of the mountain beaver are listed in appendix 1.

DESCRIPTION

The material under External Characters and Pelage was based on the examination of specimens in the National Museum and specimens obtained from Olympia, Wash., with references drawn from Coues (1877b).

External Characters

The general body conformation of the mountain beaver is stout, compact, and cylindricoid. The average adult weighs about 2-1/2 pounds and measures slightly more than a foot, resembling a tailless muskrat (Ondatra zibethica).

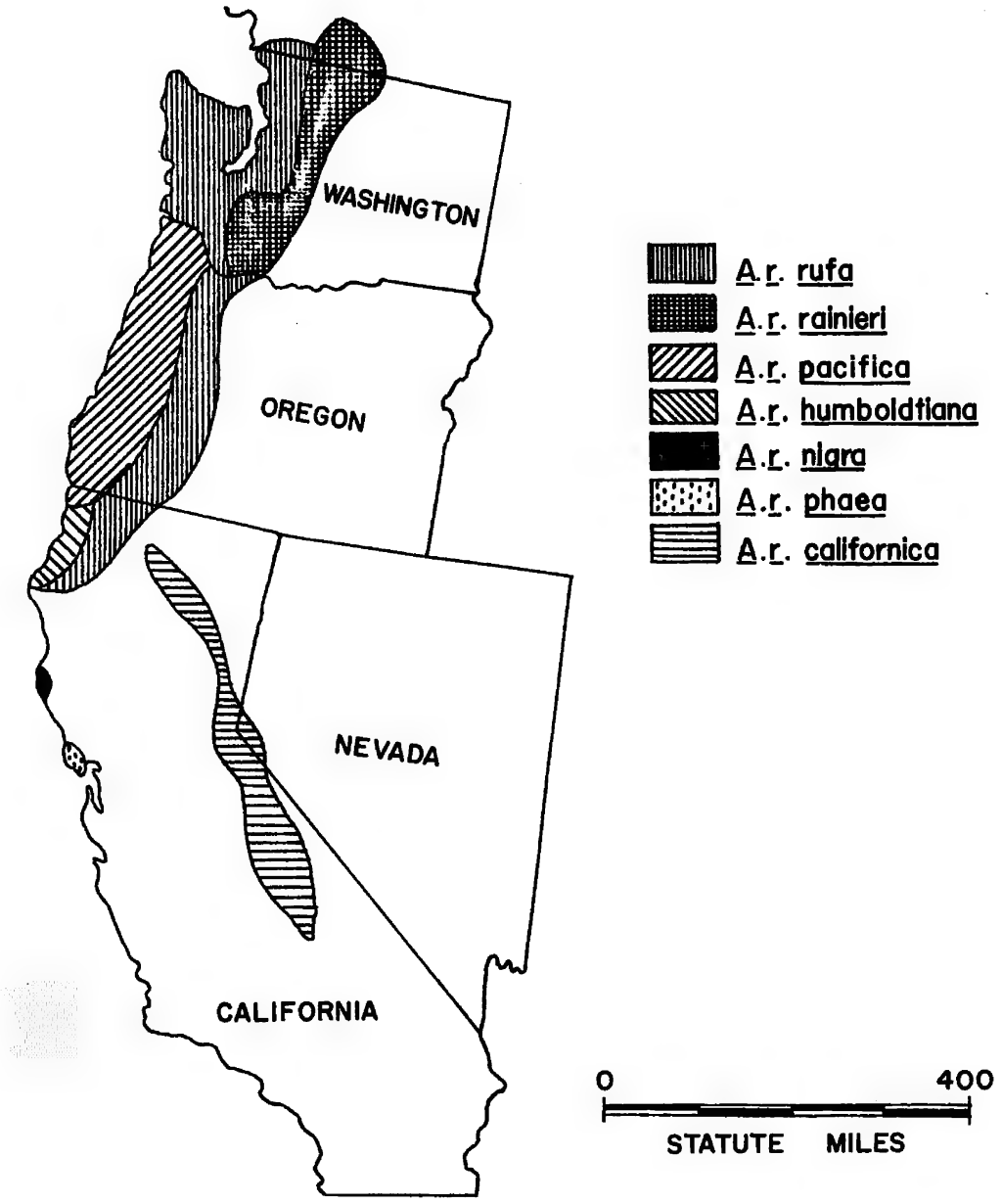

Figure 2. Distribution of the Seven Races of the Mountain Beaver

The head is relatively broad, massive, compressed laterally, and noticeable for the flatness of its upper surface which continues to the shoulders without a depression of the nape, and with scarcely any constriction of the sides of the neck behind the ears. The peculiar shape of the head as a whole may be correlated with the preponderance of right angles and planes which the skull exhibits (see frontispiece).

The undersurface of its retreating chin is nearly flat, with the distal end broadly convex. The muzzle is blunt and hairy except for the margin of the external nares and the cleft of the upper lip. The opening of the mouth looks contracted from the hairy thick lips which partially expose the incisors. Cheek pouches are absent. The long, stiff, and numerous vibrissae are mostly colorless. Some of the longest ones, when laid backwards, may reach beyond the shoulders.

The diminutive eyes (diameter between the canthi, about 1/4 inch), situated about halfway in a line between the extremity of the snout and the middle of the ear, appear sunken and inexpressive.

The ears of moderate size, rounded above, lobate below with an antigral fold, and resembling the human ear in form, are uniformly furred with soft hairs. They are situated upon the most prominent postero-superior aspect of the head rising about as high as the fur surrounding them.

The fore and hind pentadactyl limbs are short and approximately equal. The palm of the forefoot has five tubercles and the sole of the hind foot has six. The forelimbs are close to the head. The back of the forefoot has uniformly short adpressed hairs like those on the concavity of the ear. The smooth palm of the hand and the undersides of the digits are naked and pinkish. The functional and opposed thumb, indicating true prehensile powers of the hand, bears both a small, stumpy, compressed obtuse claw, and a true claw. The remaining digits are long and well formed. The third digit is the longest; the second and fourth subequal, and the fifth is the shortest with the tip of this claw being a little longer than the base of the fourth digit claw. The compressed and slightly curved claws are nearly as long as their respective digits. The nonwebbed hind foot is a little longer than the forefoot including the claws. The heel is naked and flat. The digits and claws are like those of the forefoot except the fore claws are much longer and stouter, adapted for digging.

The distinctive feature of the external anatomy of the mountain beaver is its cylindrical tail, a mere stump, about 1/4 inch shorter than the forefoot. It is furred like the body. Though vestigial, it is not concealed as is the vestigial tail of certain other rodent species.

Pelage

The pelage looks like that of an unprimed rabbit, but coarser in texture due to the large number of interspersed guard hairs. These guard hairs are more noticeable on the limbs and ventral side of the body. The scattered guard hairs on the dorsal and lateral surfaces are black, giving an ochraceous sheen to the reddish-brown underfur. The guard hairs on the lower lateral and central sides of the body are almost colorless. They appear black at the base but white-tipped, giving a smoke-gray cast to these parts. Both sexes have similar pelage color. The pelage of the young has less red and more gray. At the base of the ear is a conspicuous white spot.

The mammae number three pairs: The pectoral (just anterior to the axilla), the thoracic, and the abdominal.

Molt

The only known reference to molt is in Taylor's revision (1918). He wrote:

> "There is but one molt annually in Aplodontia. Pelage renewal begins in July and August, rarely as early as June, and continues for two or three months. There is no hard and fast manner of molting. The hair usually begins coming in on the sides posteriorly and on the back of the head and neck about the same time. From these centers the molt spreads until the new pelage covers the body, the hair of the shoulders and rump being the last to be renewed dorsally. In some examples the molt proceeds somewhat irregularly. The molt of the underparts lags behind that of the upperparts. The new pelage is longer and sometimes slightly different in coloration from the worn pelage it replaced. Thus in Aplodontia rufa pacifica, the fresh pelage is more richly colored than the worn pelage; in A. r. californica, it is a trifle browner; and in A. r. phaea, it is a little more intensely colored. Differences in coloration and general appearance are small, however, and in several forms of Aplodontia, as at present represented in collections examined, cannot be shown to exist at all."

Abnormal Colors

Jewett (1935) reported a distinctly albino mountain beaver from Yacolt, Wash.; a partial albino from Chelan County, Wash., and a melanistic specimen from Clackamas County, Oreg. Anderson and Russell (1957) cited a partially albino specimen from King County, Wash. The only two abnormally colored mountain beaver specimens in the National Museum are No. 30889, a partially albino adult male collected by C. P. Streator on September 14, 1891, at Sauk, Wash., and No. 192635, a melanistic adult male collected by C. A. Allen on August 2, 1886, at Point Reyes, Calif.

Internal Characters

Viewed from the side, the skull on top is remarkably flat and parallel with the base; the lower edge of the occiput is horizontal and perpendicular to the longitudinal axis of the skull. The palate continues in a straight horizontal line from the incisors to the ends of the pterygoids.

Seen from above, the skull shows a nearly equilateral triangle. The rostrum is stout and sloping. The zygomatic process curves outward and backward, then contracts to the jugal forming a deep arch. The auditory bulla is flack-shaped. The massester muscle originates principally beneath the infraorbital foramen and no part of the muscle reaches the rostrum. The skull is also remarkable in that it lacks postorbital processes.

The generic word Aplodontia comes from two Greek words: haploos (simplex) and odontos (teeth), meaning simple teeth. The cheek teeth are modified hypsodont. All the molars are rootless and prismatic. The pattern of the molar crowns is simple, except the anteriormost upper premolar which is a small simple cylinder lying obliquely against the anterolingual corner of the second premolar. The second premolar and three molars are set obliquely outward, decreasing in size from the second premolar to the last molar. Each tooth has a prominent style on the labial side of the upper teeth and on the lingual side of the lower teeth. The anterior faces of the stout incisors are smooth, convex in both directions, and their sides bevelled. Dental formula for the mountain beaver is:

$$I\frac{1}{1},\ C\frac{0}{0},\ P\frac{2}{1},\ M\frac{3}{3} \times 2 = 22 \text{ (fig. 3).}$$

REPRODUCTION

The mountain beaver is monestrous, has a low reproductive rate, and usually does not bear young before the second year. The mating season usually begins in late February or early March. Pfeiffer (1958), who studied reproduction in the female mountain beaver, found that the estrous female has hypertrophied nipples, a greatly swollen vulva, and an enlarged uterus and cervix.

By estimating age from the degree of closure of the distal epiphyseal femoral suture and measuring estrous uteri, Pfeiffer classified four age classes of females. He classified them as:

I. Short yearlings (all under 1 year)
II. Long yearlings (between first and second year), nulliparous
III. End of second year or early in their third year between December and July
IV. No sutures, hence full grown and parous females.

The majority of parous females were over 2 years old.

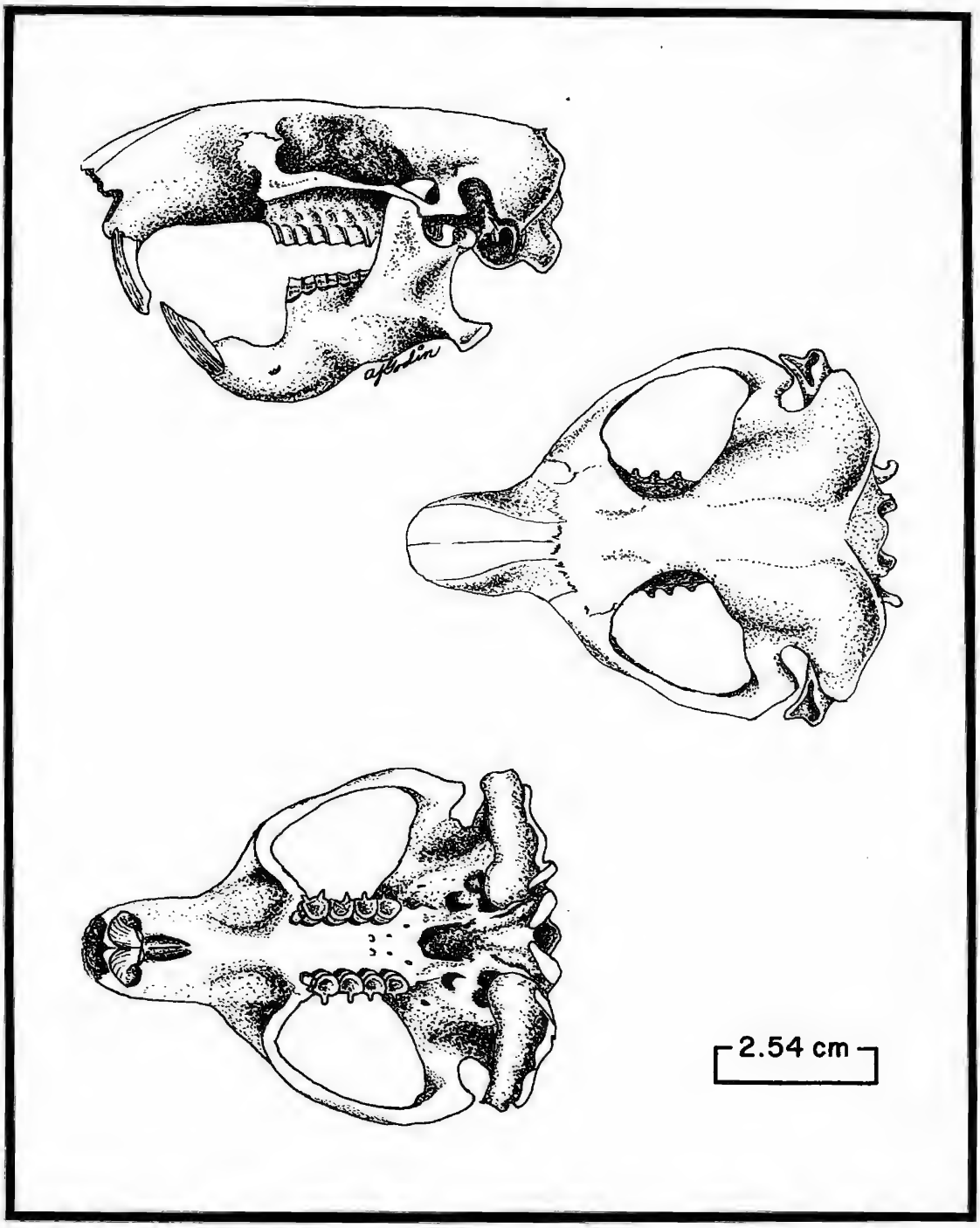

Figure 3. Views of the skull of the mountain beaver.

Pfeiffer estimated the fertility and fecundity of females by ovarian and uterine examinations. He found little loss of ova or embryos between ovulations and implantation, suggesting a very short estrous period. He also found that all females in a given population ovulate about the same time each year so that there is a very sharply defined and extremely limited breeding season within a population. These criteria enabled him to determine that estrus occurs within a short period of from 5 to 7 weeks in mid- or late winter.

Gestation Period

From data which gave dates of ovulation and parturition, Pfeiffer estimated that the gestation period is 28 to 30 days. He found early embryos during the last half of February and large fetuses during the first half of March. Scheffer (1929) reported early stages of pregnancy in mid-March, and found that by April 25th, of 23 parous females 11 were nursing young, and 12 were pregnant. He examined 26 females on April 5, of which 11 were pregnant. Of the 15 nonpregnant females, Scheffer thought 6 to be matured but unmated, and 9 to be immature yearlings. He suggested that the gestation period was about 30 days.

The difference in embryo stages between Pfeiffer and Scheffer's findings is due to different geographic ranges of individual populations. Pfeiffer's embryos were from a Point Reyes, Calif. population; whereas Scheffer's were from the Puget Sound Country in Washington.

Parturition

Cramblet and Ridenhour (1956) live-trapped a pregnant female mountain beaver in Humboldt County, Calif., on March 15, 1954. Palpation showed that it was about 1 week prepartum. They determined the prepartum period by comparison with fetuses of rodents of comparable size.

On March 19, the authors observed that the animal lactated slightly. On the following day they noted wavelike contraction of the female's abdominal muscles which appeared to be due to fetal movements. Similar contractions were observed on the following 2 days. On March 23, they observed that the female pressed her forefeet against the genital region and gnashed her teeth. This activity of 2 to 18 minutes duration was repeated periodically for the next 1-1/2 hours. Immediately before parturition, the female positioned herself on her haunches and lowered her head between her hind legs. When the tail of the first fetus appeared, she assisted its birth by pressing her forefeet around the vulva and licking the region. The birth of the first fetus was completed in 4 minutes. The head of the second fetus appeared 21 minutes later, and the birth process was completed in 5 minutes. One minute later the tail of the third fetus appeared, and the birth was completed in 2 minutes.

The authors assumed that the long period of time between the birth of the first and second fetus and the short time between the second and third fetus could possibly be attributed to the location of the fetuses in the uterine tubes. They stated that there might possibly be a lag between the descent and appearance of the single fetus from one uterine tube and the descent and appearance of the two fetuses from the opposite tube.

Number of Young at Birth

Lord (1866) asserted that the mountain beaver has from 4 to 6 young at a birth and 2 litters a year. Lum (1878) reported from 3 to 5 young per litter and that the weaned young make their appearance during June.

Scheffer (1929) examined data from 16 litters, and found 7 litters of twins (44 percent) and 9 litters of triplets (56 percent). Seton (1928) said that the litter size is usually 2, but occasionally may number 3 or 4.

Young at Birth

In their observation on parturition in the mountain beaver, Cramblet and Ridenhour (1956) reported that the young at birth are naked, blind, and helpless. The vibrissae are apparent. The auricular openings are sealed, and the external ear formation is observable but not extended. The front toes are well developed, but the hind toes are mere stubs. The tail is very noticeable. The eyes are closed during the first 10 days.

For the three young examined at birth by Cramblet and Ridenhour, the average body length was 87.7 millimeters and the average body weight 27.0 grams.

Lactation

Pfeiffer (1958) thought that lactation did not continue beyond 2 months after parturition since he found juveniles of that age with vegetable matter in the stomach; at this time they have been reported to leave their mother. He stated that in nursing females the pectoral mammae are often the most used, and the thoracic pair are commonly used, while the abdominal pair are sometimes not used.

Physiology of the Mammae

Pfeiffer (1955) wrote that pregnant, lactating, and nonpregnant postovulatory mountain beaver females exhibit dense patches of black hairs around the nipples. He found that estrogen directly or indirectly applied either by inunction or injection thickened the epidermis of the nipple and surrounding area. The estrogen also stimulated the hair follicles in this area to rapid growth and hyperpigmentation resulting in hairs larger and darker than before estrogen stimulation.

Because the mountain beaver is closely related to the ground squirrels, Pfeiffer speculated that the mammary glands in the mountain beaver represent an expression of the latent capacity of the mammary epidermal tissue to produce special hairs associated with lactation, as is found in the monotremes. He further speculated that the production of mammary hairs by the mountain beaver may be a "physiological relict" that has been lost by the more advanced mammals including man.

HABITS

Food

The mountain beaver has a voracious appetite. It feeds on almost any available plant growing near its burrow. Scheffer (1929) stated that herbaceous plants are eaten whole, whereas woody plant structures are discarded after the bark has been pulled off for food. Bracken fern (Pteridium aquilinum), sword fern (Polystichum munitum), salal (Gaultheria shallon), Oregon grape (Mahonia nervosa), and thimbleberry (Rubus parviflora) are some preferred foods, but willow (Salix), Douglas-fir (Pseudotsuga menziesii), western hemlock (Tsuga heterophylla), other conifers, meadow grasses, and garden and truck crops are also eaten. In captivity, they are known to eat a wide variety of vegetables and fruits. Some plants known to be eaten by the mountain beaver are listed in appendix 2.

Feeding

Camp (1918) said that the mountain beaver has a slow and cumbersome gait and seldom ventures far from its burrow. He also said that in order for the animal to forage in a suitable clump of vegetation, it will dig a tunnel directly into the area, and from its burrow entrance issue short trails to the vegetation to transport cut stems or fronds to the burrow entrances. Scheffer (1929) wrote that harvested cuttings varied in length from a few inches to several feet and are dragged to the burrow entrances or other safe retreat. The longer material is cut into smaller sections before being carried into the burrows to be eaten or stored. He stated that when dragging long shoots on a foraging trip the animal holds its head more or less to one side to avoid tramping on its load. Shorter pieces are lifted from the ground with the head well raised.

Manner of Feeding

Camp (1918) observed the manner of feeding of a captive mountain beaver. He wrote:

> "The rodent usually sits back upon its short tail, with the back curved, the hind feet extending out in front, soles forward, and the forepaws grasping the stem, root or leaf. The short first finger is used like a human thumb and the large callosities on the palms aid in holding an object so firmly that it can be retained easily in one hand." (fig. 4)

Stephens (1906) mentioned that the hind feet as well as the forefeet are used in grasping.

Figure 4. Manner of feeding of the mountain beaver (Photo by Weyerhaeuser Co.)

Haymaking

Gibbs (1860) was the first to note that mountain beaver gather their cuttings into neat piles which they lay out to wilt or dry on logs or stones near their burrow entrances. Bretherton (1895) and Lyon (1907) confirmed the peculiar "haymaking" habit of the mountain beaver. Stephen (1906) stated that the animal carries the cured hay into its burrow as soon as it becomes well wilted, but not dried. Camp (1918) and Scheffer (1929) concluded that the cured hay is used for nest building material rather than for food consumption. However, Seton (1928) said that this may be true in the summer, when succulent plants abound. He pointed out that it is well known that the nesting instinct of rodents is closely akin to the food storage instinct. He believed that the mountain beaver sleeps on its supplies, and uses them as food in the winter, when deep snow covers the ground. Hamilton (1939) wrote that the mountain beaver begins its haymaking activity in early August.

Refection

Pilleri (1960) and Ingles (1961) observed refection of captured mountain beavers. They stated that upon emerging from a rest period, the animal went to its fecal pile to defecate. When each oblong hard pellet was passed, the animal would take the pellet into its mouth and toss it onto the fecal pile. One mountain beaver which had returned to defecate was observed eating a pellet from its fecal pile. Another mountain beaver retrieved and chewed its last discarded pellet.

In examining the large intestines of three adult mountain beavers, Ingles found that the soft pellets were fewer and roughly four times the volume of the hard pellets. The soft pellets were composed of light green, finely macerated material. The hard pellets were dark green and brown. In the stomach of another animal, he found unmistakable clumps of soft pellet material mixed with the harsher, dark-green stomach contents.

Tree Climbing

Lewis and Clark (1905) wrote that the mountain beaver climbs trees to trim and, like a ground squirrel, burrows into the ground. Stephens (1906) reported that the animal climbs bushes and small trees, trimming off branches 3 or 4 feet from the ground. Seton (1928) reported that the hunters claim that the animal can and does climb trees, and this was disputed by the naturalists who claimed that it can no more climb trees than can a mole or muskrat. Grinnell and Storer (1924) wrote that the mountain beaver is not known to climb. Scheffer (1929) mentioned that there was no evidence that the mountain beaver can climb trees. He stated, however, that the rodent climbs tall shrubs and saplings to a height of 12 to 15 feet from the ground, leaving stubs of trimmed branches as ladder rounds. The trimming process usually includes the terminal shoot.

Ingles (1960) observed mountain beavers which were held captive in an enclosure. He reported that the rodent can and does climb trees to a height of 20 feet from the ground. He wrote:

> "Climbing was accomplished by advancing one foreleg, then the opposite hind leg, in succession. The forefeet actually grasp the small branches and the hind feet are simply placed on them. Where branches are lacking, the animal applies the claws of both feet to the bark of the trunk in climbing. The smooth bark of the small white firs at the site of the colony shows unmistakable claw marks 12 feet from the ground ... Sometimes, after a twig was cut off, it was allowed to fall to the ground, but more often it was carried down in the animal's mouth as it descended the trunk head first. The descent was made more slowly than the ascent, as the branches, or their remaining stubs, were again utilized to the utmost as rungs of a ladder. The forefeet grasped them tightly as the hind feet extended around the trunk as far as possible to provide the brake."

Tree Descending

Scheffer (1929) stated that the animal leaves the stubs of branches attached to the trunk to facilitate its descent. Dalquest (1948) saw a mountain beaver that was several feet up in a sapling. He said that the animal had clipped the branches close to the trunk and was desperately reaching with its hind feet for the missing branches. When he came near the animal, it squealed, tumbled to the ground and scurried frantically to its burrow. Harry D. Hartwell (personal communication) saw mountain beaver repeatedly drop from heights of four feet in the enclosures at the Olympia Forest Research Center.

Swimming

Anthony (1916) said that the mountain beaver swims well and rapidly, showing no fear of water. Ingles (1947) wrote that the animal is a fine swimmer, and is often mistaken for a muskrat when seen in mountain streams. He thought that the mountain beaver swims from choice. Dalquest (1948) stated that the animal enters the water rapidly with much noise. He said it wades rather than swims.

Drinking

The mountain beaver drinks a considerable amount of water. Brooks (1899) wrote that its burrows always lead to water. Anthony (1916) said that a captive mountain beaver drank large amounts of water when it was given to him.

Voice

The mountain beaver has been credited with a real voice. Suckley and Gibbs (1860) wrote of a man who heard mountain beaver, early in the

morning, emit whistling sounds similar to those of the prairie dog (Cynomys ludocicianus). Lord (1866) heard whistling in the evening which he attributed to the mountain beaver. Matteson (1877) said the rodent made a booming noise. Lum (1878) said it growled when caught in a trap. Anthony (1916) stated that angry mountain beaver utter a husky querulous note somewhat like a cough. Scheffer (1929) wrote:

> "The whistling sounds credited to them by careless observers can be traced to other sources, probably to the sooty grouse (Dendragapus obscurus) in one case and to the marmots of the Cascades and the Olympics in the other."

Kindschy and Larrison (1961) wrote that a mountain beaver captured in a trap and presumably in pain, uttered a soft whining and sobbing sound. Wendell E. Dodge (personal communication) said that mountain beavers emit a high-pitched squeal when fighting with each other in pens, but never heard them make noises when not disturbed.

Perception

Due to its fossorial habits, the mountain beaver's sight and hearing are limited. Camp (1918) wrote:

> "Sight and hearing seem to be relatively defective in the mountain beaver. The individual comes in contact with its underground environment chiefly through the sense of feeling, and this is markedly developed all over the body. The slightest touch upon a hair will be responded to instantly by quick jerking movements. The sense of smell seems to be good, for the animal has a way of frequently raising its nose to sniff; also the scent glands are well developed."

Scheffer (1929) wrote:

> "They readily leave their burrows in the twilight of evening to follow a trail of apple peelings or other tempting bait. Judging from observation of their mode of life, it is probable that the sense of smell plays but little part in enabling them to detect the presence of an enemy. On the other hand, it is no doubt their chief means of recognizing their kind, for they possess an unmistakable body odor, though it is not so pronounced as in the case of the Mustelidae, including martens, weasels, otters, and skunks."

Sociability

The mountain beaver is not sociable. Anthony (1916) stated that although it has been asserted that the mountain beaver is gregarious and lives in colonies of several individuals, this he thought to be a few individuals. Scheffer (1929) found no evidence that the animal possessed any social traits. He wrote:

"Though they sometimes live together in such numbers that their burrows fairly honeycomb the ground, the activities of the individual seem to concern only itself and are no way related to the common good. It can not properly be said of them, therefore, that they live in colonies. In the struggle for existence they are merely crowded together sometimes by the necessities of environmental conditions - food, shelter, soil. When kept in captivity they do not huddle together in their common fear and dejection, but appear grouchy, each resenting fiercely the slightest contact with its fellow."

Harry D. Hartwell (personal communication) said that mountain beaver fight continually when two animals are placed in small holding pens. He observed captive mountain beaver fighting in a 1/4-acre enclosure. Even provision of separate housing units failed to prevent fighting between captive animals.

ACTIVITY

Daily

The nocturnal nature of the mountain beaver is well documented. Rafinesque (1817) stated that the animal is chiefly nocturnal. Grinnell and Storer (1924) referred to the animal as reclusive and nocturnal. Dailey (1936) alluded to the mountain beaver's nocturnal activity. Scheffer (1929) believed that the rodent is active in its burrow during the day and leaves it only at night. Dalquest (1948) found that, although principally active at night, the mountain beaver is frequently seen during the day in the autumn.

Ingles (1959) studied the daily activity of the mountain beaver. He found that during the summer the rodent had 6 or 7 feeding periods within each 24 hours. He stated that the animal was 50 to 60 percent active at night, since food was obtained at equal risk. He did not think that the nocturnal activity of the mountain beaver was attributed to the absence of nocturnal predators -- the coyote (Canis latrans) and the great horned owl (Bubo virginianus). Pilleri (1960) said that the mountain beaver had poor eyesight and was affected by bright light, which soon caused it to become drowsy.

Seasonal

Cooper (1860) wrote of an old Indian hunter who frequently saw mountain beaver running on top of the snow in the Nisqually Valley, Washington. Suckley (1860) learned from the Nisqually Indians that the animal moves about a little during the winter but does not become decidedly active until late in the spring. Matteson (1877) believed that the mountain beaver hibernates. Bretherton (1895) said that it did not hibernate. Camp (1918) stated that the rodent is active during the winter, even in the high mountains. Howell (1924) wrote that the mountain beaver was active

beneath the snow during the winter. Scheffer (1929) affirmed that it is active during the winter, at least at the lower altitudes where it was commonly observed. He wrote:

> "Under a snow covering of a foot or more they will burrow extensively, usually though not always, working so close to the ground as to leave a trail or path scratched in the soil. Sometimes the snow burrows lead to the surface, especially near logs or stumps, and the animals come out and travel about on the crust. This is indicated by tracks and by the marks of girdling and gnawing on the bark of shrubs and young trees. They also have been observed wandering about at evening twilight on the snow crust of open fields."

Dalquest (1948) said that the animal is more restricted in habits in the winter, and is rarely seen during the day. He mentioned that the spring revealed elongated earth cores, about 6 to 8 inches in diameter and 2 to 4 feet long, as evidence of mountain beaver activity under the snow.

ENEMIES

Predators

The mountain beaver is a source of food among some predators. Lord (1866) regarded the raccoon (Procyon lotor) as a possible enemy of the mountain beaver. Anthony (1916) speculated that, owing to the dense cover of vegetation, the animal was not very extensively preyed upon by hawks and owls. Scheffer (1929) thought that certain predaceous birds and mammals were not abundant enough to take a toll of the mountain beaver. Pfeiffer (1953) caught five weasels (Mustela frenata) and one mink (Mustela vison) while trapping for mountain beaver in southern British Columbia. He believed that the weasels were hunting for mountain beaver kits, and doubted that any weasel, excepting mink, could kill an adult mountain beaver. Taylor and Shaw (1927) recorded that the mountain lion (Felis concolor) occasionally preyed on the mountain beaver in Washington. Young (1958) reported that the bobcat (Lynx rufus) preyed on the rodent in spring and summer.

Other predators that have been cited are coyotes (Canis latrans), gray foxes (Urocyon cinereoargenteus), badgers (Taxidea taxus), and fishers (Martes pennanti).

Parasites

The mountain beaver has its share of parasites. Victor B. Scheffer (personal communication) reported three species of fleas from a mountain beaver which Dr. William L. Jellison described for him. These included 28 Dolichopsyllus stylosus, 1 Hystrichopsylla sp., and 1 Trichopsylloides oregonensis. Information on other parasites reported is listed in appendix 3.

ECOLOGY

Habitat

The mountain beaver is found at elevations from sea level to 10,000 feet. Scheffer (1929) stated that it inhabits almost any wooded situation where soil conditions permit easy burrowing. It occurs on hillsides, old burns, logged-off land, along roadside clearings, and on the tops of high ridges and mountains (fig. 5). The animal is dependent upon an abundant supply of boreal plants of riparian growth. It is most abundant near springs, streams, and damp places. Dalquest (1948) wrote that clearings are the principal habitat of the mountain beaver.

Common signs of mountain beaver are trimmed and pruned bushes, shrubs, and trees, and earth honeycombed with tunnels.

Burrows and Nests

The mountain beaver has extensive irregular tunnels forming a network of passages a few inches beneath the ground surface with many entrances and roof openings (cave-in). Unlike the pocket gopher (Thomomys) or the mole (Scapanus), the mountain beaver does not repair the roof openings. However, it keeps its tunnels clear and uses the roof openings to push out excavated earth and debris (fig. 6). Ingles (1959) said that at times the animal may emerge from any one of the many roof openings and feed unobserved.

Camp (1918) wrote that the unplugged burrows are so well concealed beneath tangled vegetation that the presence of the rodent is often unknown to persons resident in the immediate vicinity. The main tunnels are 4 to 8 inches in diameter. Connected to the tunnels are enlargements for nests or for temporary food storage.

Scheffer (1929) excavated a nest. It was located under the roots of a fallen tree. The nest was oval, 20 inches high and 13 inches wide. It contained leaves and stems of bracken fern laced together with grass and small twigs. The nest was protected from flooding by a basin 6 inches beneath the nest. Two drainage tunnels led away from this basin.

Abundance

Wherever the mountain beaver lives, it digs extensive tunnels. Each tunnel system has many burrow openings (fig. 7). The grouping of tunnel systems and openings in an area suggest a flourishing colony and that mountain beavers are abundant.

Camp (1918) wrote that overcrowded conditions may occur in one area, while nearby areas of similar environment remain unoccupied. From an area of 100 by 500 feet, containing about 100 burrow entrances, he trapped 11 mountain beavers in 169 trap-nights. In the last 46 trap-nights no mountain beavers were captured. Camp concluded that the 11 captures approximated the total population of that particular area of the colony.

Figure 5. Mountain beaver habitat in clear-cut area of Capitol Forest, Grays Harbor County, Washington (Photo by Wendell E. Dodge)

Figure 6. Mountain beaver clearing tunnel of earth and debris
Capitol Forest, Grays Harbor County, Washington
(Photo by Wendell E. Dodge)

Figure 7. Mountain beaver in a burrow entrance, Capitol Forest, Grays Harbor County, Washington. Vegetation is huckleberry and salmonberry (Photo by Wendell E. Dodge)

In another area of the colony 6 mountain beavers were caught in 92 trap-nights. Grinnell and Storer (1924) said that the population of mountain beaver in a series of burrows consisted usually of a pair of adults.

Hartwell (personal communication) caught 8 mountain beavers (6 males and 2 females) in two successive nights. Four males and 1 female were caught on the first night. He used 53 steel traps in the square 1-acre plot site.

ECONOMIC SIGNIFICANCE

Damage

Dalquest (1948) mentioned that the mountain beaver is more of a nuisance than a pest. Cahalane (1947) said that in its normal habitat the rodent rarely does any harm, although it invades gardens, cutting off plants and carrying them to its burrow. It is known to undermine roadbeds and irrigation ditches.

Scheffer (1952) wrote that the mountain beaver gnaws the tender bark of saplings or larger tree bases and roots below the snow, killing the plants or causing them to be blown over. Such damage occurs usually in late winter or early spring, when the food stores may have become depleted. King (1958) made a 10-year study of damage to planted Douglas-fir and naturally seeded conifers. He attributed two-thirds of the mortality of these trees to wildlife. The greatest single damage was caused by the mountain beaver, which destroyed approximately 40 percent of the planted trees and 8 percent of the natural seedlings. Staebler, Lauterbach, and Moore (1954) pointed out that mountain beaver damage to plantations with similar cover conditions varied by locality. Munger (1943) attributed plantation failure mainly to the mountain beaver.

Lawrence, Kverno, and Hartwell (1961) categorized three types of injuries to conifers: (1) stem clipping or gnawing of small seedlings; (2) branch cutting for climbing and descending; and (3) basal girdling or debarking. The debarking injury is shown by neatly scattered horizontal tooth marks and vertical claw marks. These three types of injuries have been found in individual trees.

Damage caused by the varying hare (Lepus americanus) can be distinguished from that caused by the mountain beaver: the hare rarely clips stems exceeding 1/4 inch in diameter, or taller than 2 to 3 feet; the mountain beaver frequently cuts stems exceeding 1/2 inch in diameter up to heights of 15 to 20 feet.

As Food

Gibbs (1960) reported that the Nisqually Indians placed high value upon mountain beaver meat. Suckley (1860) ate a mountain beaver, and found it excellent. He said it tasted much like chicken (Gallus gallus), and was far

superior to beaver (Castor canadensis), raccoon (Procyon lotor), or woodchuck (Marmota monax). Scheffer (1929) stated that the meat was dark-colored and possessed a certain rankness which did not commend it as a table delicacy. But this fault could be overcome by proper cooking. Ingles (1947) reported that mountain beaver flesh is tough.

As Fur

Cooper (1860) mentioned that the Nisqually used mountain beaver pelts for making robes and garments. A large number of pelts were required to make an ordinary robe. He said that the Indians palmed off mountain beaver skins for muskrat skins when dealing with inexperienced fur agents from the Hudson Bay Company. Scheffer (1929) wrote that Bureau of Biological Survey investigations, conducted in cooperation with the furriers, showed that the fur was too flat to be profitable in the fur trade. Ingles (1947) reported that the fur had little value. Even fully primed pelts were seldom worth more than 20 cents.

CONTROL

In limited areas of its range the mountain beaver becomes a problem, as in certain crop lands and in areas which are being reforested. Control measures should be directed only to these problem areas.

Because of its unwary nature, the mountain beaver is captured easily. Harry D. Hartwell, (personal communication) said that the surest method, and the only practical method, of removing mountain beavers in small areas is by trapping them. He found No. 0, 1, or 1-1/2 steel traps most effective. Hartwell wrote:

Steel Traps

> "The traps are set directly on the ground just inside the burrow entrances, or on the floor of caved in runways. They are secured by stakes or chain. The traps are placed lengthwise to the burrow. There is no need to conceal or cover the traps. They should be visited at least twice a day, in the morning and in the evening, to avoid unnecessary suffering of the captured animals, and to insure maximum effectiveness.
>
> "Conibear" traps set upright and crosswise in the underground runways are also effective. These traps set in the runways generally catch the animals around the neck and kill them quickly. Mountain beavers caught in this manner are better for biological specimens since the fur and bones are not damaged.

Live Traps

> "Live traps are generally employed for life-history studies. The two folding traps employed are the 6- by 6- by 19-inch single door and the 6- by 6- by 24-inch double door.

"Two methods of placement are used. In the first, either type of trap is placed close to the burrow entrance. In the second method, the double-door trap is placed in an excavated portion of a main runway, usually just below ground level. During inclement weather, the traps should be covered with weatherproof material. In fair weather, they may be covered with foliage, bark or sod. Covering keeps the captive animal relatively quiet and gives the appearance of an extension of the burrow. Sufficient quantity of salal, sword fern, or apples should be placed in the traps for sustenance of captive animals.

Baiting

"On larger areas baiting with poison bait is more effective where trapping would be impractical. The best known bait is fresh apple cut into 1-inch cubes, dusted with powdered strychnine alkaloid at the rate of 1 ounce to 16 pounds of bait. Two or three poison baits are placed in the burrows appearing to be most active. Active burrows are detected by their worn appearance or by accumulations of fresh cuttings at their entrances. It is advisable to prebait the active burrows to about 1 week before baiting with poison bait, to accustom the mountain beaver to the bait. Other fruits, vegetables, and pelletized baits have been used with little success."

TECHNIQUES

Age Determination

The pelage of the young mountain beaver is soft and gray. As the animal matures the pelage becomes harsher and its color changes to brown or red. Pfeiffer (1958) used the degree of closure of the distal epiphyseal femoral suture to determine four age classes (see Reproduction). He found little difference comparing pelves of the sexes. The space between the iliac crests was more narrow in first-year animals than in older animals. In young the union between the pubes consisted of cartilage jointed with ligament. In adults the cartilage was replaced by bone.

Males -- Pfeiffer (1956) found that the baculum in juvenile males is about 11 mm. long; in yearling males (18 months old) about 21 mm., and about 30 mm. in adults. The adult baculum is deeply bifurcated at its distal tip.

Females -- Pfeiffer (1958) reported that juvenile, anestrous, and parous females taken prior to the breeding season did not show the dense patches of black hairs around the nipples shown by pregnant, lactating, and nonpregnant females with corpora lutea.

Sex Determination

Determining the sex of mountain beaver is not difficult. It is easy to distinguish the prepuce of the males from the vulva of the females. In addition, the large (about 1 inch or more in length) bifurcated penis of the male is readily extended. Males are also slightly larger than females. The conspicuous black hairs around the nipples of parous and lactating females, is a practical external character that distinguishes the sexes. Taylor (1918) stated that these black hairs are inconspicuous or lacking in the winter.

IN CAPTIVITY

Harry D. Hartwell (personal communication) wrote that mountain beaver can be held in captivity for extended periods of time in small enclosures of about 6 square feet. Pfeiffer (1953) discounted some of the statements made in the literature that the mountain beaver is difficult to keep in captivity. He kept several of these rodents for long periods of time (6 months or more) in small laboratory cages designed for rabbits and guinea pigs. Also, mountain beaver have recovered completely from such operations as ovariectomy and epididymal biopsy.

Large amounts of water and an assortment of vegetation are necessary to keep the rodent in good health.

PROSPECTS

Much has been written on the toxonomy, paleontology, and life history of the mountain beaver. Walter P. Taylor summarized the full taxonomic history of the genus, and McGrew reviewed the paleontology of the rodent. Monographic studies of the life history include those of H. E. Anthony, Charles L. Camp, Theo. H. Scheffer, and L. G. Ingles. E. W. Pfeiffer studied reproduction in the mountain beaver, and various parasitologists contributed information. But there is a dearth of knowledge regarding its ecology. We need to know more about its adaptation to new environments, direct effects on man's activities, depredation, food habit studies, predatory relationships, movements (immigration and emigration), population dynamics, methods of inventory, and carrying capacity to mention a few. For example, E. W. Pfeiffer, W. C. Mungesser, and D. A. Iverson (1960) found that the mountain beaver has a very limited ability to concentrate urine. Pfeiffer (personal communication) suspected that this inability limits the species' range to areas of a constant adequate water supply. Could this inability be a factor which limits the distribution of the mountain beaver in North America?

One essential step in the process of research is the combing of the literature. The purpose of this review was to summarize the available references for use in future research on the mountain beaver. This is followed by intensive field investigations.

Appendix 1 -- THE LOCALITY AND RANGE OF THE SEVEN RACES OF THE MOUNTAIN BEAVER

1. Brown mountain beaver, Aplodontia rufa rufa (Rafinesque)

Type Locality. Neighborhood of the Columbia River, Oreg. Specimens from Marmot, west slope of Mount Hood, Clackamas County, regarded as typical by Taylor (1918).

Range. From Chilliwack-Sumas region on western side of Cascade Mountains in southwestern British Columbia southward through western Washington, between Puget Sound and Cascade Mountains, to Columbia River; marginal localities are Bellingham, Forks of Skykomis River, north bend and mouth of Kalama River.

2. Mount Rainier mountain beaver, Aplodontia rufa rainieri (Merriam)

Type Locality. Paradise Creek, south side of Mount Rainier, Pierce County, Wash. Altitude 5,200 feet.

Range. Cascade Mountains in southwestern British Columbia, from Skagit on western slope near international boundary north to Hope; only two records from drier eastern slope of Cascades -- east side of summit of Hope-Princeton Trail at 5,600 feet, and Stirling Creek near Headley in middle Similkmeen Valley at 1,700 feet (Anderson, loc. cit.); southward through higher Cascade Mountains of Washington (Dalquest, loc. cit.) and Oregon to Siskiyou and Trinity Mountain regions of northwestern California, and thence southwest as far as Rio Dell, Eel River, Humboldt County, regarded as rufa by Grinnell (1933).

3. Pacific mountain beaver, Aplodontia rufa pacifica (Merriam)

Type Locality. Newport, mouth of Yaquina Bay, Lincoln County, Oreg.

Range. Coast region of Oregon from Columbia River (Astoria) southward to near Smith River, Del Norte County, Calif. Finley (1941).

4. Humboldt Bay mountain beaver, Aplodontia rufa humboldtiana (Taylor)

Type Locality. Carlotta, Humboldt County, Calif.

Range. Extreme northern humid coast belt, from Requa, Del Norte County, south to vicinity of Carlotta, Humboldt County, and interiorly to vicinity of Weitzpek, Humboldt County; vertical range, below 1,000 feet; zonal range, Canadian and Transition, Grinnell (1933).

5. Point Arena mountain beaver, Aplodontia rufa nigra (Taylor)

Type Locality. Point Arena, Mendocino County, Calif.

Range. Known only from type locality, where it is found within an area of approximately 24 square miles.

6. Point Reyes mountain beaver, Aplodontia rufa phaea (Merriam)

Type Locality. Point Reyes (probably somewhere near present town of Inverness), Marin County, Calif.

Range. Humid coast belt of Marin County, from 5 miles west of Inverness east to Langunitas and south to four miles south of Olema; area inhabited, approximately 110 square miles; vertical range below 1,000 feet; zonal range, Transition. Grinnell (1933).

7. Sierra Nevada mountain beaver, Aplodontia rufa californica (Peters)

Type Locality. Assumed to be the Sierra Nevada of California. Grinnell (1913); specimens from Blue Canyon, Placer County, in central Sierra Nevada may be regarded as typical. Taylor (1918) and Hall (1941).

Range. Sierra Nevada, north to Mount Shasta and south as far as Clover Creek, Sequoia National Park, Tulare County; vertical range, from 4,600 feet (Blue Canyon, Placer County); zonal range, Canadian and Hudsonian. Grinnell (1933). Recorded also eastward to Washoe and Ormsby Counties, Nevada. Hall (1946).

Appendix 2 -- SOME FOODS OF THE MOUNTAIN BEAVER

Scientific Name	Common Name
Pteridium aquilinum	Bracken fern
Polystichum munitum	Sword fern
Tsuga heterophylla	Western hemlock
Pinus contorta	Lodgepole pine
Pinus lambertiana	Sugar pine
Abies concolor	White fir
Pseudotsuga menziesii	Douglas fir
Salix spp.	Willow
Sorbus occidentalis	Mountain ash
Prunus emarginata	Wildcherry
Rubus vitifolius	Dewberry
Rubus parviflorus	Thimbleberry
Rubus spectabilis	Salmonberry
Vaccinium parvifolium	Huckleberry
Castanopsis chrysophylla	Chinquapin
Rhododendron occidentale	Azalea
Corylus californica	Hazel
Ribes nevadense	Sierran currant
Cornus nuttallii	Pacific dogwood
Cornus pubescens	Creek dogwood
Ceanothus cordulatus	Snowbush
Libocedrus decurrens	Incense-cedar
Gaultheria shallon	Salal
Lupinus longipes	Lupine
Epilobium latifolium	Fireweed
Valeriana sitchensis	Sitka valerian
Mertensia laevigata	Lungwort
Veratrum viride	False hellebore
Lysichiton americanum	Skunkcabbage
Gramineae	Grasses
Mahonia nervosa	Oregon grape
Dicentra cucullaria	Dutchman's breeches

Appendix 3 -- SOME PARASITES OF THE MOUNTAIN BEAVER

	Scientific Names	Reported by
Ectoparasites		
Beetles	*Leptinillus aplodontiae*	Ferris, G. F. 1918
Fleas	*Ceratophyllus stylosus*	Baker, C. F. 1904
	Dolichopsylla stylosus	Baker, C. F. 1904
	Epitedia scapani	Hubbard, C. A. 1940
	Epitedia jordani	Hubbard, C. A. 1943
	Hystrichopsylla hubbardi	Augustson, C.F. 1953
	Hystrichopsylla schefferi mammoth	Chapin, C. V. 1921
	Hystrichopsylla schefferi schefferi	Chapin, E. A. 1919
	Paratyphloceras oregonensis	Hubbard, C. A. 1943
	Trichopsylloides hubbardi	Ewing, H. E. 1938
	Trichopsylloides oregonensis	Ewing, H. E. 1938
Mites	*Acomatacanus hirsutus*	Gould, D. J. 1956
	Alphalaelops aplodontiae	Radford, C. D. 1951
	Ichoronyssus hubbardi	Jameson, E. W., Jr. 1949
	Trombicula aplodontiae	Brennan, J. M. 1946
	Laelaps aplodontiae	Radford, C. D. 1951
	Trombicula jewetti	Brennan, J. M. 1946
Ticks	*Ixodes augustus*	Cooley, R. A. and
	Ixodes rugosus	G. Milton 1945
Endoparasite		
	Taenia tenuicollis	Locker, B. 1955

BIBLIOGRAPHY

Allen, Joel A.
1892. Visitors guide to the collection of mammals in the American Museum of Natural History. American Museum of Natural History, New York, 89 p.

Alston, Edward R.
1876. On the classification of the order Glires. Proceedings, Zoological Society London, p. 61-98.

Anderson, Rudolph M.
1946. Catalogue of Canadian recent mammals. National Museum of Canada, Ottawa, Bulletin 102, Biological Series No. 31, p. 168.

Anderson, Sydney, and Robert J. Russell
1957. Color and dental abnormalities in an Aplodontia. Transactions, Kansas Academy of Sciences 60(2):181.

Anonymous.
1855. California Academy of Natural Sciences, Meeting for September 24, 1855. Proceedings, California Academy of Natural Sciences 1, 71 p.
1865. California Academy of Natural Sciences, Meeting for September 18, 1865. Proceedings, California Academy of Natural Sciences 3, 224 p.
1866. Report of C. Hart Merriam: account of a new species Aplodontia major that is larger and heavier than Aplodontia rufa. American Naturalist 20(7):662.

Anthony, H. E.
1916. Habits of Aplodontia. Bulletin, American Museum of Natural History, New York, Vol. 35, p. 53-63.
1928. Field book of North American mammals. G. P. Putnam's Sons, New York, 674 p.

Asdell, S. A.
1946. Patterns of mammalian reproduction. Comstock Publishing Company, Ithaca, New York, 437 p.

Audubon, J. J., and J. Bachman
1854. The quadrupeds of North America, New York Audubon 3, 348 p.

Auguston, Gustaf F.
1942. Ectoparasite host records from the Sierran region of east central California. Bulletin, Southern California Academy of Science 40(3):147-157.
1953. Some new fleas Siphonaptera of western United States. Bulletin, Southern California Academy of Science 52(3):119-126.

Bailey, Vernon
1932. Mountain beaver Aplodontia rufa californica, Yosemite National Park. Sierra Club Bulletin 17(1):19
1936. The mammals and life zones of Oregon. North American Fauna 55, 416 p.

Baird, Spencer F.
1857. Report on Zoology. I. Mammals. U. S. Pacific Railroad Exploration and Survey, Vol. 8, 757 p.

Baker, Charles F.
1904. A revision of American Siphonaptera, or fleas, together with a complete list and bibliography of the group. Proceedings, U. S. National Museum 27, p. 365-469.

Blair, Frank W., Albert P. Blair, Pierce Brodkorb, Fred R. Cagle, and George A. Moore
1957. Vertebrates of the United States, McGraw-Hill Book Company, New York, 667 p.

Blyth, Edward
1840. Mammalia in Cuvier's animal kingdom. Orr, London, p. 38-152.

Bonaparte, Charles Lucien
1831. Saggio di una distribuzione metodica degli animali vertebrati. Giornale Arcadico di Scienze Lettre ed Arti 49, 77 p.

Brandt, Johannes F.
1855. Beiträge zur nähern Kenntniss der Säugethiere Russlands. Mem. Acad. Imp. Sci., St. Petersbourg, ser. 6 and 7, 365 p.

Brennan, James M.
1946. Two new species of Trombicula: I. montanensis and I. aplodontiae (Acarina, Trombiculidae) from northwestern United States. Journal of Parasitology 32(5):441-444.

Bretherton, B. J.
1895. Some Oregon mammals: The mountain boomer Haplodon rufus. Oregon Naturalist 2, p. 123-125.

Brooks, Allan
1899. The sewellel Aplodontia rufa. Recreation 2, p. 258-259.
1926. Past and present big game conditions in British Columbia and the predatory mammal question. Journal of Mammalogy 7(1):37-40.

Brown, D. E.
1930. Additional notes from a country home. The Murrelet 11(2):18-19.

Bryant, W. E.
1891. A provisional list of the land mammals of California. Zoe 1:353-360.
1892. Recent additions to the North American land mammal fauna. Zoe 3:201-223.

Burroughs, Raymond D.
1961. The natural history of the Lewis and Clark Expedition. Michigan State University Press, East Lansing, 340 p.

Burt, William H., and Richard Philip Grossenheider
1952. A field guide to the mammals. Houghton Mifflin Company, Boston, 200 p.

Butcher, Devereux
1955. Seeing America's wildlife in our national refuges. The Devin-Adair Company, New York, 338 p.

Cahalane, Victor H.
1947. Mammals of North America. The Macmillan Company, New York, 682 p.

Camp, Charles L.
1918. Excavations of burrows of the rodent Aplodontia, with observations on the habits of the animal. University of California Publications in Zoology 17(18):517-536.

Carl, Clifford G., C. J. Guiguet, and George A. Handy
1952. A natural history survey of the Manning Park Area. British Columbia Provincial Museum, Handbook No. 9, p. 76.

Cassin, J.
1858. Mammalogy and ornithology. U. S. Exploration (Wilkes) 3, 466 p.

Chapin, Charles V.
1921. Remarks on the genus Hystrichopsylla Tasch, with description of a new species, Siphonaptera. Proceedings, Entomological Society Washington 23(2):25-27.

Chapin, Edward A.
1919. New species of North American Siphonaptera. Bulletin, Brooklyn Entomological Society 14(2):49-62.

Cockrum, E. Lendell
1962. Introduction to mammalogy. The Ronald Press Company, New York, 455 p.

Cooley, Robert A., and Glen Milton
1945. The genus Ixodes in North America. National Institute of Health, Bulletin 184, U. S. Public Health Service, 246 p.

Cooper, J. G.
1860. Report upon the mammals collected on the Survey, U. S. Pacific Railroad Exploration and Survey, Vol. 12, Book 2, Part 3(1):73-88.
1868. Zoology in Cronise: The natural wealth of California. Bancroft, San Francisco, p. 434-501.

Cope, Edward D.
1878. On some characters of the Miocene fauna of Oregon. Palae, Bulletin 30, 16 p.
1883. The extinct Rodentia of North America. The American Naturalist 17, p. 43-57.

Couch, Leo K.
1925. Rodent damage to young trees. The Murrelet 5(2):39
1926. List of small mammals from the lower Puget Sound region. The Murrelet 7(2):29-30.

Coues, Elliott
1877a. The mountain boomer, or showtl. American Naturalist 11, 434 p.
1877b. "Haplodontidae" in monographs of North American Rodentia. Report, U. S. Geographical Survey of the Territories 11(9):543-601.

Cowan, Ian McTaggart, and Charles T. Guiget
1956. The mammals of British Columbia. British Columbia Provincial Museum, Department of Education, Victoria. Handbook No. 11, 413 p.

Cramblet, Howard M., and Richard L. Ridenhour
1956. Parturition in Aplodontia. Journal of Mammalogy 37(1):87-90.

Dalquest, Walter W.
1941. Ecologic relationships of four small mammals in western Washington. Journal of Mammalogy 22(2):170-173.
1948. Mammals of Washington. University of Kansas Publications, Museum of Natural History, Lawrence, Vol. 2, 444 p.

Dalquest, Walter W., and Victor B. Scheffer
1945. The systematic status of the races of the mountain beaver Aplodontia rufa in Washington. The Murrelet 25(3):34-37.

Davis, Jared J.
1941. Notes on a captive mountain beaver. The Murrelet 22(3):60-61.

Dice, Lee R.
1932. Mammals collected by F. M. Gaige in 1919 at Lake Cushman and vicinity, Olympic Peninsula, Washington. The Murrelet 13(2):47-49.

Dolph, C. I., H. A. Braun, and E. W. Pfeiffer
1962. The effect of vasopressin upon urine concentration in Aplodontia rufa (sewellel) and the rabbit. Physiological Zoology 35(3):263-269.

Doran, David
1954. A catalogue of the Protozoa and Helminths of North American rodents. The American Midland Naturalist 53(1):118-128.

Douglas, David
1836a. A sketch of a journey to the northwestern parts of the continent of North America during the years 1824-1827, in Hooker, W. J. Companion to Botanical Magazine, London, Curtis, 2, p. 83-140.
1836b. Account of Mr. Douglas' second visit to the Columbia; his excursions in California; and his visit to Mouna Roa in the Sandwich Islands; with particulars respecting his death. Ibid 2, p. 146-178.
1914. Journal kept by David Douglas during his travels in North America, 1823-1827. London, Wesley, 364 p.

Eadie, W. Roberts
1954. Animal control in field, farm, and forest. The Macmillan Company, New York, 257 p.

Ellerman, John R.
1940. The families and genera of living rodents. Vol. 1. Rodents other than Muridae. British Museum (Natural History), London, 689 p.
1949. The families and genera of living rodents. Vol. 3, Part 1. British Museum (Natural History), London, 210 p.

Elliot, Daniel Giraud
1899. Catalogue of mammals from the Olympic Mountains, Washington; with descriptions of new species. Publication of the Field Columbian Museum, Zoological Series, Vol. 1, p. 241-276.
1901. A synopsis of the mammals of North America and the adjacent seas. Publication of the Field Columbian Museum, Zoological Series, Vol. 2, p. 111-114.
1903. A list of mammals obtained by Edmund Heller, collector for the museum, from the coast region of northern California and Oregon. Publication of the Field Columbian Museum, Zoological Series, Vol. 3, p. 184-185.
1905. A check list of mammals of the North American continent, the West Indies and the neighboring seas. Publication of the Field Columbian Museum, Zoological Series, Vol. 6, p. 126-128.
1907. A catalogue of the collection of mammals in the Field Columbian Museum. Publication of the Field Columbian Museum, Zoological Series. Vol. 8, p. 188-190.

Ewing, Henry E.
1938. Two new genera and one new species of Siphonaptera. Proceedings, Entomological Society Washington 40(4):93-95.

Ewing, Henry E. and Irving Fox
1943. The fleas of North America. Classification, identification, and geographic distribution of these injurious and disease spreading insects. Miscellaneous Publication No. 500, U. S. Department of Agriculture, 142 p.

Ferris, Gordon F.
1918. An apparently new species of Leptinillus (Coleoptera, Leptinidae). Canadian Entomologist 50(4):125-128.

Finley, Robert B., Jr.
1941. Geographic variation in the rodent Aplodontia rufa. The Murrelet 22(3):45-51.

Forsyth Major, Charles I.
1893. On some Miocene squirrels, with remarks on the dentition and classification of the Sciurinae. Proceedings, Zoological Society, London, p. 179-215.

Friant, M.
1937. Le pretendu genre Pseudaplodon de Gerrit S. Miller(Aplodontia asiatica Schlosser) au pontien de Mongolie. Ann. Mag. Nat. Hist., 19, p. 456-462.

Fry, Jack F.
1961. Musculature and innervation of the pelvis and hind limb of the mountain beaver. Journal of Morphology 109(2):173-197.

Furlong, Eustace L.
1910. An aplodont rodent from the Tertiary of Nevada. University of California Publication Bulletin, Department of Geology 5(6):397-403.

Gabrielson, Ira N.
1938. Controlling rodents and other small animal pests in Oregon. Federal Cooperative Extension Service, Oregon State College, Corvallis, Extension Bulletin 512, 24 p.

Geoffroy Saint-Hilaire, Isidore
1826. La marmotte rousse Arctomys rufa. Dict. Class. d'Histoire Naturelle, Paris, Baudouin Fères 10, 642 p.

Gerrard, E.
1862. Catalogue of the bones of Mammalia in the collection of the British Museum (Natural History), London, 296 p.

Gervais, P.
1854. Histoire naturelle des mammifères. Paris. Curmer, 420 p.

Giebel, Christoph G.
1855. Die Säugethiere in zoologischer und paleontogischer Beziehund um fassend dargestellt. Leipzig, Ambrosius Abel, 1108 p.
1859. Die Naturgeschichte des Thierreichs. 1. Die Säugethiere. Leipzig, Wigand, 522 p.

Gill, T.
1872. Arrangement of the families of mammals with analytical tables. Smithsonian Miscellaneous Collection, 11, 98 p.

Glass, Bryan P.
1951. A key to the skulls of North American mammals. Burgess Publishing Company, Minneapolis, 54 p.

Gould, Douglas J.
1956. The larval trombiculid mites of California (Acarina. Trombiculidae). University of California Publications in Entomology 11(1):1-115.

Gray, John E.
1843. List of the specimens of Mammalia in the collection of the British Museum. British Museum (Natural History), London, 216 p.

Griffith, E.
1827. The animal kingdom. London, Whittaker, Vol. 5, 391 p.

Grinnell, Joseph
1913. A distributional list of the mammals of California. Proceedings, California Academy of Sciences 4(3):265-390.
1915. The vertebrate fauna of the Pacific Coast. Nature and Science on the Pacific Coast, p. 104-114.
1916. An analysis of the vertebrate fauna of the Trinity region of northern California. University of California Publications in Zoology 12:399-410.
1923. A systematic list of the mammals of California. University of California Publications in Zoology 21(10):321.
1933. Review of the Recent mammal fauna of California. University of California Publications in Zoology 40(2):194-195.

Grinnell, Joseph, Joseph S. Dixon, and Jean M. Linsdale
1930. Vertebrate natural history of a section of northern California through the Lassen Peak region. University of California Publications in Zoology 35, 594 p.

Grinnell, Joseph, and Tracy I. Storer
1924. Animal life in the Yosemite, University of California Press, Berkeley, 669 p.

Hall, E. Raymond
1931. On the occurrence of certain mammals in extreme southwestern Washington. The Murrelet 12(1):22.
1941. The type specimen of Aplodontia rufa californica (Peters). The Murrelet 22(3):50-51.
1946. Mammals of Nevada. University of California Press, Berkeley, 710 p.
1957. Vernacular names for North American mammals north of Mexico. University of Kansas, Museum of Natural History, Miscellaneous Publication No. 14, 16 p.

Hall, E. Raymond, and Keith R. Kelson
1959. The mammals of North America. The Ronald Press Company, New York, Vol. 1, p. 290-292.

Hall, Frank S.
1932. A historical resume of exploration and survey - mammal types and their collectors in the State of Washington. The Murrelet 13(3):63-91

Hamilton, William J., Jr.
1939. American mammals: their lives, habits, and economic relations. McGraw-Hill Book Company, New York, 434 p.

Harlan, R.
1825. Fauna Americana. Finley, Philadelphia, p. 308-309.

Harvey, E. B.
1955. Placentation in Ochotonidae and Aplodontidae. Ph.D. Thesis, University of California, Berkeley.

Henderson, Junius, and Elberta L. Craig
1932. Economic mammalogy, Charles C. Thomas, Springfield, Illinois, 294 p.

Herlocker, Emmett
1950. Mountain beaver, biological curiosity. Audubon Magazine 52(6):387-390.

Herms, William B.
1950. Medical entomology, with special reference to the health and well being of man and animals. The Macmillan Company, New York, 643 p.

Hill, John Eric
1935. The cranial foramina in rodents. Journal of Mammalogy 16(2): 121-128.

Holder, J. B.
1877. History of the American fauna. American Museum of Natural History.

Holland, George P.
1949. The Siphonaptera of Canada. Technical Bulletin No. 70, Dominion of Canada, Department of Agriculture, 306 p.

Hooper, Emmet T.
1944. San Francisco Bay as a factor influencing speciation in rodents. Miscellaneous Publications, Museum of Zoology, University of Michigan, No. 59, University of Michigan Press, Ann Arbor, 99 p.
1949. Faunal relationships of recent North American rodents. Miscellaneous Publications, Museum of Zoology, University of Michigan, No. 72, University of Michigan Press, Ann Arbor, 28 p.

Howell, A. Brazier
1924. The mammals of Mammoth, Mono County, California. Journal of Mammalogy 5(1):25-36.

Hubbard, C. Andresen
1922. Some data upon the rodent Aplodontia. The Murrelet 3(1):14-18.
1940. A check list of the fleas of the Pacific Northwest,(Washington, Oregon, Northern California, and Northwestern Nevada), with notes from southern California. Pacific University Bulletin 37(4):1-4.
1943. The fleas of California with check lists of the fleas of Oregon, Washington, British Columbia, Alaska, Idaho, Nevada, Arizona. Pacific University Bulletin 39(8):1-12.
1945. My last new North American fleas. Entomology News 65(7): 169-175.
1947. Fleas of western North America; their relation to the public health. The Iowa State College Press, Ames, 533 p.

Ingles, Lloyd G.
1947. Mammals of California. Stanford University Press, Stanford, 258 p.
1954. Mammals of California and its coastal waters. Stanford University Press, Stanford, 396 p.
1959. A quantitative study of mountain beaver activity. The American Midland Naturalist 61(2):419-423.
1960. Tree climbing by mountain beavers. Journal of Mammalogy 41(1):120-121.
1961. Reingestion in the mountain beaver. Journal of Mammalogy 42(3):411-412.

Jacobs, [?]
1884. Animals of the Puget Sound region. American Field 21(19):456.

Jameson, E. W. Jr.
1949. A new mite Ichoronyssus hubbardi from the mountain beaver (Aplodontia rufa Rafinesque). Journal of Parasitology 35(2):109-115.

Jameson, E. W. Jr., and James M. Brennan
1957. An environmental analysis of some ectoparasites of small forest mammals in the Sierra Nevada. California Ecological Monographs 27(1):45-54.

Jellison, William L.
1945. A new mite Laelaps aplodontiae from Aplodontia. Journal of Parasitology 31(6):373-374.
1945. A suggested homolog of the os penis or baculum of mammals. Journal of Mammalogy 26(2):146-147.

Jewett, Stanley G.
1935. An albino mountain beaver. The Murrelet 16(1):18.

Johnson, Murray L., and Sherry Johnson
1952. A check list of mammals of the Olympic Peninsula. The Murrelet 33(3):32-37.

Johnson, Murray L., and Merrill J. Wicks
1959. Serum protein electrophoresis in mammals; taxonomic implications. Systematic Zoology 8(2):88-95.

Kellogg, Louise
1910. Rodent fauna of the late Tertiary beds at Virgin Valley and Thousand Creek, Nevada. University of California Publication Bulletin, Department of Geology 5(6):421-437.
1912. Pleistocene rodents of California. University of California Publication Bulletin, Department of Geology 7:151-168.
1914a. Aplodontia chryseola, a new mountain beaver from the Trinity region of northern California. University of California Publication in Zoology 12(5):295-296.
1916. Report upon mammals and birds found in portions of Trinity, Siskiyou and Shasta Counties, California. University of California Publications in Zoology 12(13):369-372.

Kellogg, Louise, and Walter P. Taylor
1914b. A previously undescribed Aplodontia from the middle north coast of California. University of California Publications in Zoology 12(6):297-300.

Kindschy, Robert R. Jr., and Earl J. Larrison
1961. Observations on a captive mountain beaver. The Murrelet 42(1):1-3.

King, James E.
1958. Development of a stand of coniferous reproduction and interplanted Douglas-fir. Northwest Science 32(1):1-8.

Lantz, D. C.
1917. Destroying rodent pests on the farm. Yearbook, U. S. Department of Agriculture, Separate 708 (1916), 18 p.

Lawrence, William H., Nelson B. Kverno, and Harry D. Hartwell
1961. Guide to wildlife feeding injuries on conifers in the Pacific Northwest. Western Forestry and Conservation Association, Portland, Oregon, 44 p.

Lesson, René Primevère
1827. Manuel de mammalogie, ou histoire naturelle des mammifères. Paris, Roret, 442 p.

Lewis, M., and W. Clark
1814. History of the Lewis and Clark expedition. Paul Allen Edition, Philadelphia, Bradford, 522 p.
1876. An account of the various publications relating to the travels of Lewis and Clark, with a commentary on the Zoological results of their expedition. Elliot Coues in U. S. Geological and Geographical Survey of the Territories, (2), Bulletin No. 6, p. 417-444.
1904. Original journals of the Lewis and Clark expedition, 1804-1806. 8 Volumes. Thwaites' Edition, Dodd, New York.

Lewis, Thomas H.
1949. The morphology of the pectoral girdle and anterior limb in Aplodontia. Journal of Morphology 85(3):533-588.

Lilljeborg, Wilhelm
1866. Systematisk öfversigt af de gnagande Däggdjuren Glires, Upsala, Kongl. Akademischen, Boktryckeriet, 59 p.

Locker, Betty
1955. The identification of Taenia tenuicollis Rudolphi, 1819, in North America. Journal of Parasitology 41(1):51-56.

Lord, John K.
1866. The naturalist in Vancouver Island and British Columbia. 2 Volumes, London, Bentley, 358 p.

Loring, J. A.
1900. Sewellel, Oregon base of Mount Jefferson. Forest and Stream 54:504-505.
1948. Mountain beaver, range, habits, characteristics. Naturalist Magazine 41(7):355.

Lum, S. K.
1878. The sewellel or show'tl. American Naturalist 12:10-13.

Lyon, Marcus Ward, Jr.
1907. Notes on mammals collected at Mount Rainier, Washington. Smithsonian Miscellaneous Collection 50:89-92.

Lyon, Marcus Ward, Jr., and W. H. Osgood
1909. Catalogue of the type-specimens of mammals in the National Museum, including the Biological Survey collection. U. S. National Museum Bulletin 62, 325 p.

Mailliard, Joseph
1923. Field work among the birds and mammals of the northern coast of California in 1921. Proceedings, California Academy of Sciences, Fourth Series 12(1):1-26.

Marsh, O. Charles
1877. New vertebrate fossils. American Journal of Science 3(14):249-256.

Martin, Alexander C., Herbert S. Zim, and Arnold L. Nelson
1951. American wildlife and plants: a guide to wildlife food habits: the use of trees, shrubs, weeds, and herbs by birds and mammals of the United States. McGraw-Hill Book Company, New York, 236 p.

Matteson, F. S.
1877. The mountain boomer, or showtl. American Naturalist 11:434-435.

Matthew, William D.
1904. New or little known mammals from the Miocene of South Dakota. Bulletin, Museum of American Natural History 20(2):246-265.
1907. A lower Miocene fauna from South Dakota. Bulletin, Museum of American Natural History 23:169-219.
1910. On the osteology and relationships of Paramys, and the affinities of the Ischyromyidae. Bulletin of American Natural History 28:43-72.

McGrew, Paul O.
1941. The Aplodontoidea. Geological Series, Field Museum of Natural History of Chicago 9(1):1-30.

McLean, D. D.
1925. Afield with the nature guides. Yosemite Nature Notes 4(19):103.

Merriam, C. Hart
1886. Description of a new species of Aplodontia (Aplodontia major, sp. nov.) from California. Annals, New York Academy of Sciences 3(10):312-328.
1897. The mammals of Mount Mazama, Oregon. Mazama 1:204-230.
1899a. Description of six new rodents of the genera Aplodontia and Thomomys. Proceedings, Biological Society Washington 13(1):19-21.
1899b. Results of a biological survey of Mount Shasta, California. U. S. Department of Agriculture, Division of Biological Survey, North American Fauna 16, 179 p.

Merriam, John C.
1911. Tertiary mammal beds of Virgin Valley and Thousand Creek in northwestern Nevada. Part11, Vertebrate Faunas, University of California Publications in Geology 6:199-304.

Merriam, John C., and W. J. Sinclair
1907. Tertiary faunas of the John Day region. University of California Publications in Geology 5:171-205.

Miller, Gerrit S. Jr.
1912. List of North American land mammals in the National Museum, 1911, U. S. National Museum Bulletin 79, 455 p.
1923. List of North American Recent mammals. U. S. National Museum Bulletin 128, p. 429-436.

Miller, Gerrit S. Jr., and Remington Kellogg
1955. List of North American Recent mammals. U. S. National Museum Bulletin 205, p. 178-180.

Miller, Gerrit S. Jr., and J. A. G. Rehn
1901. Systematic results of the study of North Aermican land mammals to the close of the year 1900. Proceedings, Boston Society of Natural History 30:1-352.

Minding, J.
1829. Ueber die geographische Vertheilung der Säugetheire. Berlin, Enslin, 104 p.

Munger, T. T.
1943. Vital statistics for some Douglas-fir plantations. Journal of Forestry 41(1):53-56.

Murie, Olaus J.
1958. A field guide to animal tracks. Houghton-Mifflin Company, Boston, 374 p.

Murphy, J. M.
1876. The hunting fields of the Pacific Coast. Capturing the showtl. Rod and Gun, May 20, p. 121.
1877a. Swellel or showtl. Forest and Stream, Vol. 9, p. 44.
1877b. Shewelel or showtl. The Field, London, Vol. 49, p. 486.

Murray, A.
1866. The geographical distribution of mammals. London, Murray, 420 p.

Nelson, Edward W.
1918. Wild animals of North America. National Geographic Society, Washington, D. C., p. 385-612.

Newberry, J. S.
1857. Report upon the mammals, in Zoological Report, in U. S. Pacific Railroad Exploration and Survey 6:35-72.

Orr, Robert T.
1949. Mammals of Lake Tahoe, California, California Academy of Sciences, San Francisco, p. 102.

Osborn, Henry F.
1910. The age of mammals in Europe, Asia and North America. The Macmillan Company, New York, 635 p.

Palmer, E. Lawrence
1949. Fieldbook of natural history, McGraw-Hill Book Company, New York, 664 p.

Palmer, Ralph S.
1954. The mammal guide. Doubleday and Company, Garden City, New York, 384 p.

Palmer, T. S.
1904. Index generum mammalium: a list of the genera and families of mammals. U. S. Department of Agriculture, Division of Biological Survey, North American Fauna 23, 984 p.

Parker, Harry C.
1952. Mammals of Yosemite National Park. Yosemite Nature Notes 31(6):52-105.

Peale, T. R.
1948. Mammalia and ornithology. U. S. Exploration Expedition (Wilkes). Sherman, Philadelphia, 338 p.

Peters, Wilhelm C.
1864. Neue Arten der Säugethiergattungen Geomys, Haplodon, und Dasypus. Non. k. preuss. Akad. Wiss., Berlin, p. 177-180.

Petrides, George, and James Huss
1940. Yosemite animals - Aplodontia on Sherpherd's Crest. Yosemite Nature Notes 19(4):31.

Pfeiffer, E. W.
1953. Animals trapped in mountain beaver (Aplodontia rufa) runways, and the mountain beaver in captivity. Journal of Mammalogy 34(3):396.
1954. Reproduction of a primitive rodent, Aplodontia rufa. Ph. D. Thesis, University of California, Berkeley.
1955. Hormonally induced mammary hairs of a primitive rodent, Aplodontia rufa. Anatomical Record 122(2):241-256.
1956. The male reproductive tract of a primitive rodent, Aplodontia rufa. Anatomical Record 124(4):629-635.
1958. The reproductive cycle of the female mountain beaver. Journal of Mammalogy 39(2):223-235.

Pfeiffer, E. W., W. C. Nungesser, D. A. Iverson, and J. F. Wallerius
1960. The renal anatomy of the primitive rodent, Aplodontia rufa, and a consideration of its functional significance. Anatomical Record 137(3):227-235.

Pilleri, Von G.
1960. Zum verhalten der aplodontia rufa (Rodentia, Aplodontidea) in Gefangenschaft. Zeitschrift für Säugetierkunde, Heft Band, Berlin, p. 30-34.

Poole, Arthur J., and Viola S. Schantz
1942. Catalogue of the type specimens of mammals in the United States National Museum, including the Biological Surveys collection. U. S. National Museum Bulletin 178, 705 p.

Pratt, Henry S.
1935. A manual of land and fresh water vertebrate animals of the United States. P. Blakistons and Company, Philadelphia. 416 p.

Presnall, C.C.
1931. Yosemite animals - mountain beavers. Yosemite Nature Notes 10(7):61.

Price, W. W.
1894. Notes on a collection of mammals from the Sierra Nevada mountains. Zoe 4:315-332.

Racey, Kenneth
1922. Mountain beaver in British Columbia, Vancouver. The Ottawa Field Naturalist 36:30.

Radford, Charles D.
1951. Two new genera of parasitic mites (Acarina: Laelaptidae and Listrophoridae). Journal of Parasitology 41(1-2):102-104.

Rafinesque, C. S.
1817. Descriptions of seven new genera of North American quadrupeds in Museum of Natural Sciences. American Monthly Magazine 2:44-46.

Richardson, John
1829a. On Aplodontia, a new genus of the order Rodentia, constituted for the reception of the sewellel, a burrowing animal which inhabits the north western coast of America. Zoological Journal 4:333-337.
1829b. Fauna Boreali Americana. London, Murray, Part 1, 300 p.
1837. Report of North American Zoology, in Report 6th Meeting British Association of Advanced Science 5:121-224.

Roest, Aryan I.
1951. Mammals of the Oregon caves area, Josephine County. Journal of Mammalogy 32(3):345-350.

Scheffer, Theo H.
1926. Mountain beaver. Nature Magazine 8:165.
1929. Mountain beavers in the Pacific Northwest; their habits, economic status, and control. U. S. Department of Agriculture Farmer's Bulletin No. 1598, 18 p.
1930. Determining the rate of replacement in a species. Journal of Mammalogy 11(4):466-469.
1952. Spring incidence of damage to forest trees by certain mammals. The Murrelet 33(3):38-41.

Scheffer, Victor B.
1942. An os clitoridis from Aplodontia. Journal of Mammalogy 23(4):443.

Schlosser, Max
1884. Die Nager des europäischen Tertiars hebst Betrachtungen uber die Organisation und die geschichtliche Entwicklung der Nager überhaupt. Paleontographica, 31:1-184.

Scott, William B.
1913. A history of land mammals in the western hemisphere. The Macmillan Company, New York, 693 p.

Seton, Ernest Thompson
1928. Lives of game animals. Doubleday, Doran and Company, Garden City, New York, Vol. 4, p. 525-555.

Shaw, William T.
1934. The ability of the giant kangaroo rat as a harvester and storer of seeds. Journal of Mammalogy 15(4):275-286.
1944. Brood nest and young of two western chipmunks in the Olympic Mountains of Washington. Journal of Mammalogy 25(3):274-284.

Simpson, George Gaylord
1945. The principles of classification and a classification of mammals. Bulletin, American Museum of Natural History, Vol. 85, 350 p.

Sinclair, William John
1903. A preliminary account of the exploration of the Potter Creek cave, Shasta County, California. Science 17:708-712.
1905. New Mammalia from the Quaternary caves of California. University of California Publications in Geology 4:145-161.

Spencer, George J.
1957. North American beetles infesting mammals. Proceedings, Entomological Society, British Columbia 53:21-22.

Sperber, I.
1944. Studies on the mammalian kidney. Zoologiska Bidrag Fran Uppsala 22:249-431.

Sprague, James M.
1942. The hyoid apparatus of Neotoma. Journal of Mammalogy 23(4): 405-411.

Staebler, George R., Paul Lauterback, and A. W. Moore
1954. Effect of animal damage on young coniferous plantation in southwest Washington. Journal of Forestry 52(10):730-733.

Stephens, Frank
1906. California mammals. West Coast Nature Studies. West Coast Publishing Company, San Diego, 351 p.

Stone, Witmer, and William E. Cram
1902. American animals. Doubleday, Page and Company, New York, 318 p.

Storer, Tracy I., Francis C. Evans, and Fletcher G. Palmer
1944. Some rodent populations in the Sierra Nevada of California. Ecological Monographs 14(2):165-192.

Suckley, George
1860. Report in Zoology. Report, U. S. Pacific Railroad Exploration and Survey, Vol. 12, Book 2, Part 2, 3(2):89-106.

Suckley, George and George Gibbs
1860. Report in Zoology. Report, U. S. Pacific Railroad Exploration and Survey, Vol. 12, Book 2, Part 2, 3(2):106-389

Summer, Lowell, and Joseph S. Dixon
1953. Birds and mammals of the Sierra Nevada with records from Sequoia and Kings Canyon National Parks. University of California Press, Berkeley, p. 420-422.

Svihla, Arthur
1930. Extension of the known range of the Olympic mountain beaver. The Murrelet 11(3):75-76.

Svihla, Arthur, and Ruth Dowell Svihla
1933a. Mammals of Callam County, Washington. The Murrelet 14(2): 37-41.
1933b. Notes on the jumping mouse (Zapus trinotatus). Journal of Mammalogy 14(2):131-133.

Taylor, Walter P.
1914. A previously undescribed Aplodontia from the middle north coast of California. University of California Publications in Zoology 12:297-300.
1916a. Aplodontia humboldtiana: a new mountain beaver from the Humboldt Bay district, California. Proceedings, Biological Society Washington 29:21-24.
1916b. The status of the beavers of western North America, with a consideration of the factors in their speciation. University of California Publications in Zoology 12:413-495.
1916c. Two new aplodontias from western North America. University of California Publications in Zoology 12(16):497-501.
1918. Revision of the rodent genus Aplodontia. University of California Publications in Zoology 17(16):435-504.

Taylor, Walter P., and William T. Shaw
1927. Mammals and birds of Mount Ranier National Park. National Park Service, Department of the Interior, Washington, D.C., p. 84-87.
1929. Provisional list of land mammals of the State of Washington. Occasional Papers of the Charles R. Conner Museum No. 2. The State College of Washington, Pullman, 32 p.

Thomas, Oldfield
1896. On the genera of rodents: an attempt to bring up to date the current arrangement of the order. Proceedings, Zoological Society, London, p. 1012-1028.

Townsend, Charles H.
1887. Field notes on the mammals, birds, and reptiles of northern California. Proceedings, U. S. National Museum 10:159-241.

Trouessart, Edouard Louis
1897. Catalogus mammalium tam viventium quam fossilium. Berlin, Friedlander, p. 219-452.
1904. Catalogus mammalium tam viventium quam fossilium. Quinguenalle Supplementum: Rodentia. Berlin, Fasc. 2:289-546.

Tullberg, Tycho
1896. Zur anatomie des Haplodon rufus. Zooliska Studier, Upsala, Almquist, p. 231-351.
1899. Ueber das system der nagetiere: eine phylogenetische studie. Upsala, Akademischen Buchdruck, 514 p.

Wagler, J.
1830. Natürliches System der Amphibien mit vorangehender Classification der Säugethiere und Vogel. (Munich, Cotta), 354 p.

Wagner, Johann A.
1943. Die Säugethiere (Schreber). Suplementband 3, Abteibung, 514 p.

Wallace, A. R.
1876. The geographical distribution of animals. Macmillan, London, 2 Volumes, 607 p.

Weber, Max
1904. Die Säugethiere. Einführing in die Anatomie und Systematik der Recenten und Fossilen Mammalia. Jena, Gustav Fisher, 866 p.

Wilson, Robert W.
1938. Contributions of Paleontology (2) Pliocene rodents of western North America. Contributions to Paleontology, studies of Cenozoic vertebrates of western North America. Carnegie Institute, Washington, D. C., p. 23-71.
1949. Early tertiary rodents of North America. Contribution to Paleontology, Carnegie Institute, Washington, D. C., Publication No. 584, p. 67-164.

Winge, Herluf
1941. The interrelationships of the mammalian genera. Volume 2, Rodentia, carnivora, primates. H. Hagerups Forlag, Copenhagen, 276 p.

Wood, Albert Elmer
1937. The mammalian fauna of the White River Oligocene by W. B. Scott and G. L. Jespen. Part 2. Rodentia. Transactions, American Philo. Society 28(2):157-269.
1955. A revised classification of the rodents. Journal of Mammalogy 26(2):165-185.

Young, J. Z.
1950. The life of vertebrates. Oxford University Press, London, 767 p.

Young, Stanley P.
1958. The bobcat of North America. The Wildlife Management Institute, Washington, D.C., The Stackpole Company, Harrisburg, 193 p.

Young, Stanley P., and Edward A. Goldman
1946. The puma, mysterious American cat. American Wildlife Institute, Washington, D. C., 358 p.

Zittel, Karl A.
1893. Handbuch der Palaeontologie, Abteilung 1. Paleozoologie. Band IV, Vertebrate (Mammalia). Munich, R. Oldenbourg, 799 p.

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